## A review of natal pterylosis of passerines: useful information or avian marginalia?

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Summary.—Since Wetherbee's (1957) review of passerine natal down patterns, two new neossoptile tracts and a new region of the spinal tract have been identified. Natal down patterns provide limited support for some phylogenetic relationships based on morphological or molecular information. Ecological and geographic correlates noted in natal down patterns need to be revisited when information on more individuals and a greater array of species becomes available. The post-hatching appearance of down-like coverings of nestlings could represent a semiplume portion of the first teleoptile plumage and not natal down.

The first coat of feathers in some but not all young birds has been termed the 'natal down plumage' (Gill 1995). It is made up entirely of filamentous natal down feathers or neossoptiles. These feathers lack a shaft and consist of a tuft of barbs which extrudes on the tip of an incoming typical contour feather of the juvenile (first teleoptile) plumage. As they are fragile feathers, neossoptiles normally last for no more than a few days to a week in passerines before being permanently lost due to abrasion. Some non-passerine chicks have a dense coating of natal down as in waterfowl (Anseriformes) and fowl-like birds (Galliformes). Others, such as woodpeckers (Piciformes), kingfishers and allies (Coraciiformes) are naked at hatching being devoid of any neossoptiles (Gill 1995). In the Apodiformes, newly hatched swifts (Apodidae) are naked whilst treeswifts (Hemiprocnidae) and hummingbirds (Trochilidae) have variable amounts of neossoptiles (Collins 1978). Passerines encompass both extremes with some hatching naked (Skutch 1960, Collins & McDaniel 1989) whilst others have a thick covering of up to several hundred neossoptiles (Wetherbee 1957; CTC unpubl.).

The presence or absence of natal down has been noted, sometimes almost in passing, by many authors describing passerine chicks. In other cases the colour and length of these downs, as well as their distribution on various regions of the body, have been carefully noted (Skutch 1960, 1969, Kovshar & Gavrilov 1974, Gill 1982, 1993, 1994, Gill & Dow 1983, Smith 1985, Greeney & Gelis 2005, Greeney *et al.* 2005). Earlier studies of passerine chicks combined natal down characters (presence or absence of specific neossoptile tracts) with other characters such as mouth colour, tongue spots and size of rictal flanges to assess relationships among closely related species or genera (Neufeldt 1972, and references therein). A new phase in the study of the natal down plumage began with the detailed and quantified study of natal down distribution in North American passerines by D. K. Wetherbee (1957, 1958). This was followed by a similar survey of natal downs in African birds by M. K. Markus (1970, 1972).

My own interest in this topic was sparked by a brief encounter with Wetherbee and a copy of his monograph. I was drawn to some of the gaps in his data, particularly for some familiar family level taxa such as the Thraupidae (now Thraupinae: Burns 1997); this gap was partially closed by data on Scarlet Tanager *Piranga olivacea* presented subsequently (Wetherbee 1958). My first field season with Neotropical birds in Trinidad permitted me to gather some additional information on this diverse group (Collins 1963a). Thereafter,

during field studies of swifts in Trinidad and Venezuela, I opportunistically collected specimens of newly hatched passerines and a hummingbird (Rufous-breasted Hermit *Glaucis hirsutus*: Collins 1978). I followed Wetherbee's terminology in describing these specimens, often many years later, as time permitted or when students became interested enough to participate (Collins & Kemp 1976, Collins & Minsky 1982, Minsky & Collins 1983, Wimer & Collins 1994, Collins & Araya 1998, 2002). At this point it would be valid to ask two questions: 'What have we learned' and 'What does it tell us'?

In answer to the first question, we have learned more about the distribution of neossoptiles on passerine birds. Two new neossoptile tracts and additional regions of the spinal tract have been identified. Post-humeral neossoptiles were described for the first time by Ilyashenko (1984) from seven species of Asian passerines. A unique row of cervical tract neossoptiles was described from the Red-capped Cardinal *Paroaria gularis* (Collins & Bender 1977a). A new medial row of unpaired neossoptiles has been recognised in the pelvic region of the spinal tract (Collins & Bender 1977b). A similar medial row of neossoptiles is sometimes found anterior to the mid-dorsal region of the spinal tract and has been termed the inter-scapular region (Collins & Keane 1991, Collins & Araya 1998). There is a need for additional refinements in the description of the complex distribution pattern of the numerous neossoptiles in the capital tract of some Neotropical tyrannid flycatchers (*Elainea* and *Phelpsia*: CTC unpubl.).

What natal pterylosis tells us is less clear. It would seem logical that some informative comparisons of natal down patterns should be possible based on the new information available on additional taxa. This would include the first data on the Neotropical families Furnariidae (Collins et al. 1991, Collins & Araya 2002), Conopophagidae (Hilty 1975, Hillman & Hogan 2002), Pipridae (Collins 1982) and Tersinidae (Collins 1973) (although Swallow Tanager Tersina viridis is no longer recognised at this level: Sibley & Ahlquist 1990). However, even among the Thraupinae where there have been several studies (Collins 1963a, 1973, Ingels 1979, Levy 1997, Collins & Araya 1998), the natal down distribution of only ten species in eight genera within this large assemblage (235 species in 58 genera: Paynter & Storer 1970) have been examined in detail. In other families, such as the Furnariidae, the number of species for which there is natal down information is equally low. Even so, some ecological trends have been noted. Closed-nest building species frequently possess few or no neossoptiles (Skutch 1960, Collins & McDaniel 1989) and tropical species tend to have fewer neossoptiles than congeneric temperate zone species (Collins & Minsky 1982, Wimer & Collins 1994). However, these trends are based on only a few genera and need to be re-examined when further studies, involving more taxa, become available.

In addition to the low number of species examined, studies of natal pterylosis have generally been characterised by small sample sizes, often only a single brood, and in some cases, only a single individual. Intraspecific variation has been examined only in a few cases (Clark 1967, Collins 1990). This also needs to be given further attention.

A variety of single-character analyses have been utilised to clarify higher level relationships (Beecher 1953, Tordoff 1954, Glenny 1955, Ames 1971, Raikow 1982, 1987, Prum 1990) including some pterolographic studies (Morlion 1980, Clench 1992, 1995). However, recent molecular studies utilising cladistic approaches to phylogeny have proved far more informative in resolving avian lineages and relationships (Burns 1997, Klicka *et al.* 2007). Even so, natal pterylosis data have some utility in supporting conclusions based on behavioural, morphological and molecular characters. One early example was the generic placement of the Dull-coloured Grassquit *Tiaris obscura* in *Tiaris*, as proposed by Schwartz (1972) and Bates (1997), and not among the *Sporophila* seedeaters. *Tiaris* grassquits build globe-shaped nests with a side entrance (Bates 1997, Hilty 2003) and have sparse or no natal

down (Goodwin 1959; P. Schwartz pers. comm.). The open-cup nest *Sporophila* seedeaters have a more complete covering of neossoptiles (Collins & Kemp 1976). Natal pterylosis data also support the family level separation of the Thamnophilidae and the Formicariidae (Sibley & Ahlquist 1990). Chicks of 20 species in 14 genera of the Thamnophilidae have all been reported to be naked at hatching (Skutch 1969, Lill & ffrench 1979, Wilkinson & Smith 1997, Cadena *et al.* 2000, Wilson 2000, Christian 2001, Hennessey 2002, Armacost 2004; CTC unpubl.). Chicks of the Formicariidae generally possess a sparse to heavy covering of natal downs, especially in *Grallaria* (but see below); only chicks of *Hylopezus* and *Grallaricula* are naked at hatching (Schwartz 1957, Skutch 1969, Greeney *et al.* 2004).

Neossoptile information can also point to other situations needing further study. One example was the relationship of the Thrush-like Manakin *Schiffornis turdina* to other manakins (Pipridae). Skutch (1969) reported it to have 'copious long brownish grey down, more abundant than that on the nestlings of the majority of passerine birds.' This contrasted with the rather minimal amount of natal down in other piprids (Skutch 1969, Foster 1976, Collins 1982, Christian 2001). Later, based on morphological characters, Snow (1971) noted the genera *Manacus*, *Pipra* and *Chiroxiphia* formed a well-defined core group in the Pipridae. He also felt that the inclusion of *Schiffornis* was 'especially problematical' and it might best be included in the Tityrinae or Tyrannidae. Thereafter, syrinx morphology (Prum & Lanyon 1989) and DNA hybridisation data indicated *Schiffornis* to cluster with the 'tityra-becard group' of the Tyrannidae (Sibley & Ahlquist 1990). Like *Schiffornis*, some tyrannids possess extensive long natal down (Collins & McDaniel 1989, Collins 1990).

Neossoptiles in passerines are generally considered to be fully developed in both pattern and length at hatching (Wetherbee 1957). However, in a few cases noted by Ilyashenko (1984) it is clear that some neossoptiles, particularly in the post-humeral tract can appear 2–3 days after hatching. This was also noted for alar tract neossoptiles in a single specimen of Palm Tanager *Thraupis palmarum* (Collins & Araya 1998). In other cases, Skutch (1960) reported *Elainea* flycatchers to have a dense coat of what he termed 'secondary down' that erupts 5–7 days after hatching. These downy feathers are not attached to incoming teleoptiles and thus cannot be considered true neossoptiles. In all likelihood they represent an early-appearing semiplume portion of the first teleoptile (juvenile) plumage. This has been reported in Cypseloidine swifts (Collins 1963b) and one passerine, Blue-and-white Swallow *Notiochelidon cyanoleuca* (Arnold *et al.* 1983). Other reports of such secondary coats of natal down in *Erithacus* and *Luscinia* (Cramp 1988) need to be critically re-examined.

Similarly, the occurrence of natal down and other nestling feather coats in antpittas of the genus Grallaria needs closer examination. The hatchlings of Scaled Antpitta G. guatimalensis are reported to be 'mostly naked with some sparse down' (Dobbs et al. 2001) and hatchlings of Scrub Antpitta G. watkinsi were 'mostly naked' and 'sparse blackish down was present on most, if not all feather tracts' (Martin & Dobbs 2004). In Pale-billed Antpitta G. carrikeri natal down was 'sparse' (Wiedenfeld 1982). However, after 4-5 days posthatching, chicks of G. guatimalensis had 'dark colored down . . . present on all feather tracts except the main element of the ventral tract' (Dobbs et al. 2001). The nestling feather coat of 'dense black down' in Rufous Antpitta G. rufula (Peyre de Fabriques 1991), 'dark grey down' in White-bellied Antpitta G. hypoleuca (Price 2003), 'dense black downy plumage' and 'covered in black down' in Variegated Antpitta G. varia (Quintela 1987, Protomastro 2000), and 'dark grey down' in two subspecies of Moustached Antpitta G. alleni (Freile & Renjifo 2003) presumably all refer to a later-appearing feather coat in older nestlings and not to the sparse natal down present in hatchlings. Similarly, one Peruvian Antpitta Grallaricula peruviana nestling, estimated to be 1-2 days old, was 'bare' but when 13-14 days old was 'covered in a thick red-brown down' (Greenev et al. 2004). This later-appearing covering of downy feathers in both *Grallaria* and *Grallaricula* is clearly not natal down which is largely, if not completely, pre-hatching in its development (Wetherbee 1957). In all likelihood it is yet another case of an early-appearing semiplume portion of the incoming juvenile plumage in passerines. How widespread these semiplume feather coats are in passerines and their significance to developing chicks remains to be determined.

The functional significance of natal down remains unclear. As previously reviewed (Wetherbee 1957, and references therein), there are several suggested advantages for these feathers. Among them are (1) the provision of cryptic coloration, (2) protection from the sun's rays, (3) protection from insects, and (4) insulation for the retention of body heat. The absence (= loss?) of natal downs in a variety of closed-nest and cavity-nesting species tends to support some of these suggested functions. However, there are numerous exceptions. A variety of species, as well as the family Thamnophilidae, build open-cup nests and have naked chicks. The reverse is also true with some species that construct enclosed nests having dense coats of natal down (Collins 1990). Again, with additional information for more species on the presence, or absence, of natal downs and their distribution in passerine birds it might prove possible to better understand the adaptive significance of the natal plumage.

Considering the limited information derived thus far from studies of natal pterylosis, choices will have to be made by both field collectors and museum curators as to whether additional material will be collected and made available for future study. In an era of shrinking budgets other material with a higher potential information value, especially DNA, might have to be given priority. Even so, field workers can still make useful contributions to this field of study as shown by the many careful observations made by Skutch (1960, 1969) and others mentioned herein.

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